through a glass window is determined by its chemical composition, molecular structure, and fabrication process (*12*). Daylight seen through a window has a particular apparent brightness and color that depends on how the intensity and spectrum of the received solar radiation interacts with the window's angular and spectral transmission characteristics (*17*). The illumination quality of daylight will be altered by the spectral transmission properties of the window glass and/or diffuse reflection by interior surfaces (*18*). The specularity of reflection by opaque materials ranges from mirror-like to totally diffuse. Humans more accurately assess interior spatial dimensions when surfaces are delineated by reflectances that provide strongly contrasting luminances. However, direct sunlight reflected by glossy surfaces can cause glare.

Daylight, though ubiquitous, is rarely understood holistically.

Illuminance, color-rendering indexes, and color temperatures indicate the perceived quality of a lit environment. Warm yellowish to reddish color temperatures are alleged to be more comfortable; empirical supporting data, however, remains weak (*19*).

Advanced daylighting systems use refraction and diffraction of direct sunlight as well as diffuse daylight to improve the delivery of daylight in buildings. Anidolic systems, based on nonimaging optics, can significantly enhance the penetration of daylight into deep office spaces (*20*). Reflective louvers or blinds, prismatic films, laser-cut panels, and holographic films can be installed or attached to windows to achieve the double function of solar shading and daylight redirection. Dynamically controlling the admission of solar heat gains and daylight in buildings can maintain thermal and visual comfort in workspaces, while simultaneously mitigating demand for heating, cooling, and lighting.

The solar radiation passing through windows offers another advantage by warming surfaces in buildings: It is familiar to experience these surfaces releasing heat by convection and long-wave radiation, thus providing warmth. Such "passive" solar heating does not usually come to mind as an application of solar energy. But this commonplace phenomenon is the consequence of the spectral characteristics of glass transmitting incident short-wavelength solar radiation (up to 3,000 nm), while trapping long-wavelength thermal radiation indoors—radiation which has been emitted from solar-heated interior surfaces (~10,000 nm). More commonly recognized applications of solar energy include technological systems that collect the Sun's energy to heat fluids or produce energy, which also take advantage of the transmission properties of glass. In solar thermal collectors, a fluid flowing through a metal absorber typically transfers solar heat for applications ranging from domestic hot water up to electrical power generation. Alternatively, solar energy can also be converted directly to electricity in solar photovoltaic modules, using particular combinations of materials that absorb solar radiation at wavelength energies corresponding to quantized electron energy gaps, in order to produce an electrical current.

Conclusions

Daylight, though ubiquitous, is rarely understood holistically. The interaction of daylight with organic and physical systems, as illustrated in Figure 2, has diverse consequences, from daylight through windows, to photosynthesis in plants, to vitamin D produced by exposure of our skin to the Sun.

In this publication, architects, vision scientists, botanists, physicians, physicists, engineers, and material scientists have contributed to an eclectic range of perspectives on daylight, each of which captures only part of the complex interplay of factors implicit in this apparently simple phenomenon. The insights from these very different contexts are brought together here to provide a cross-disciplinary narrative intended to enhance our understanding of this fascinating subject.

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Light as a source of information in ecosystems

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The Sun is the primary energy source that drives the Earth's climate system. While some of the radiation emitted from the Sun is reflected back into space, a large portion is absorbed by the Earth's atmosphere and surface. Part of the longwave radiation re-emitted from the Earth is absorbed by radiatively active gases in the atmosphere—a phenomenon called the "greenhouse effect." This effect causes the Earth's surface temperature to be 33°K warmer than it would be without these gases. All parts of the Earth's climate system, including the hydrological cycle and atmospheric circulation, are driven by energy input from the Sun (*1*). Furthermore, sunlight is the central energy source for the biosphere, providing virtually all energy for life, from single cells to whole ecosystems. Except for a few peculiar ecosystems, such as the communities around hydrothermal vents on the ocean floor, all primary producers rely on sunlight for their energy supply. Plants and phototrophic bacteria (i.e., photoautotrophic organisms) convert light into chemical energy, which is distributed within the food web and supports all heterotrophic organisms including humans (*2*). Fossil fuel resources upon which current societies depend are essentially sunlight converted into biomass and accumulated over geological periods. The quantity of sunlight energy available to primary producers is thus of utmost importance—it drives virtually all biogeochemical cycles and food webs on Earth. It should be noted that only a small fraction of sunlight energy is actually converted into biomass, as many other factors (e.g., nutrient and water availability) are colimiting biological production on our planet.

Sunlight conveys not only energy, but information as well. In this respect, light quality (i.e., the presence of given wavelengths or ratios of particular wavelengths) and quantity are of pivotal significance to life (Figure 1). Light is an important cue modulating animal behavior, leading to convergent evolution, across many animal taxa, of complex light-sensing organs—including eyes—that allow for visual orientation within various light-wavelength bands. Similarly, a range of light sensors with absorption maxima at different wavelengths is important for the development and function of plants, such as triggering the time of bud

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break in spring or the shedding of leaves in autumn. In the organismal, ecosystem, landscape, and even global context, various attributes of sunlight provide important and essential information. For instance, light quantity and quality as well as their variation and alteration by organisms and communities within an ecosystem provide spatial information. Light quality (i.e., color) is central for many processes, including pollinator attraction, mating, and food location. Information is also contained in day length and the daily rhythmic variation of light quantity and quality, which both change with the seasons.

Plants are sessile organisms that need to endure and respond to day-to-day uncertainties.

In this chapter, we aim to highlight the importance of sunlight not only for delivering energy to the biosphere, but also for providing information that allows ecosystems to optimize their function and their reactions to environmental factors. We will focus on the importance of information carried by light at the largely unexplored ecosystem and biome levels. Evidence exists on the molecular, cellular, and individual levels that light information and how it is used is of central importance for understanding the processes and functions of life. We will also explore the temporal and spatial information conveyed by light and how it may increase the adaptability and plasticity of ecosystem responses, with a focus on plants and vegetation. The impact of human activity upon our planet is becoming ever more apparent, leading scientists to propose a new geological epoch: the "Anthropocene." Therefore, we also address the various ways that humans disturb or transform the information conveyed by light, and how the processing of light information in ecosystems has been and may be affected in the Anthropocene.

Information conveyed by light about recurring events

The direct effects of sunlight on energy transformation have been well described (*3*) on various organizational levels from the cell to the organ, as well as within food webs and ecosystems. However, the transfer and integration of information are not well understood, mainly at higher organizational levels—the ecosystem, the landscape, or the biome (*4*). While we know that the day–night rhythm has a strong influence on gene expression in plants via the so-called "circadian clock," we do not know to what extent these clock-triggered mechanisms affect the carbon and water balance of ecosystems.

Plants are sessile organisms that need to endure and respond to day-to-day uncertainties. Temperature, precipitation, herbivory, pathogens, and many other environmental factors affecting a plant's existence show only a limited degree of predictability. However, there is one environmental factor that varies deterministically as a function of time of year and geographical latitude: the photoperiod. Ecologists have long studied the mechanisms by which plants respond to and cope with unpredictable environmental changes. The adaptations and strategies they use to take advantage of predictable photoperiodic changes have been much less explored.

Plants can anticipate photoperiodic changes through an elaborate set of light sensors (*5*). They can anticipate dawn and dusk transitions, and can also more broadly "tell the time" and anticipate noon, midnight, and other times of day. Anticipation of the light regime is important because it allows the plant to prepare its metabolism in advance for the upcoming demands (e.g., to prepare for photosynthesis before dawn), to temporally couple or uncouple processes that are associated or incompatible, and, over the course of the year, to respond to changes in the seasons. The mechanism by which plants tell time is the circadian clock.

We have known for quite some time that not only gene expression, but also carbon and water fluxes at the leaf level, are regulated by the circadian clock (*6*). But we are only now beginning to understand the implications of this finding—and its evolutionary consequences—at the scale of the vegetation canopy and ecosystem. Diurnal variations in sunlight are the primary driver of photosynthesis, followed by variations in temperature. However, circadian regulation exerts a control of similar magnitude to that of temperature and leads to a time-dependent potential assimilation (the conversion of CO_2 to reduced organic carbon via photosynthesis) rate. This control means that, depending on the time of the day, maximum achievable rate of photosynthesis at a given set of environmental conditions such as light, temperature, and air humidity, will be different. The question then becomes, "Why it is necessary that the circadian clock increases or decreases the potential rate of photosynthesis depending on time of day?" That is, why is it that the potential assimilation rate is not consistently high over time? One could speculate that circadian regulation results in optimal resource use, such that most resources for photosynthesis are allocated at the time when they are most needed. However, recent research has shown that circadian regulation in photochemistry does not follow an optimized allocation scheme, but one that seeks to maximize carbon assimilation (*7*).

The control of stomatal conductance (i.e., the aperture of the stomata that allows CO_2 to diffuse into the leaf and water vapor to diffuse out) by the circadian clock is stronger than the control over assimilation, with recent research indicating that up to 70% of the diurnal rhythm in transpiration is driven by the circadian clock. This pattern of stomatal conductance that is consistent with a model based on maximizing carbon assimilation also leads to less conservative water use. For instance, circadian regulation is one of the major controls over nocturnal stomatal conductance, and leads to water wastage without any carbon gain. Recent work has shown how nocturnal conductance driven by the circadian clock is under genetic control; genotypes with higher conductance at predawn were able to assimilate more carbon in the initial morning hours (*8*).

Photosynthesis and stomatal conductance are not the only processes under control of the circadian clock—so is respiration (*9*). A major question concerning the circadian regulation of gas exchange is how widespread it is and under what conditions it is expressed. All plant species have the genes coding for the circadian clock, yet it is unclear whether circadian regulation of gas exchange is common to all plant species or whether the clock control over gas exchange is suppressed under certain conditions, such as in the understory (the vegetation layer(s) below the main forest canopy).

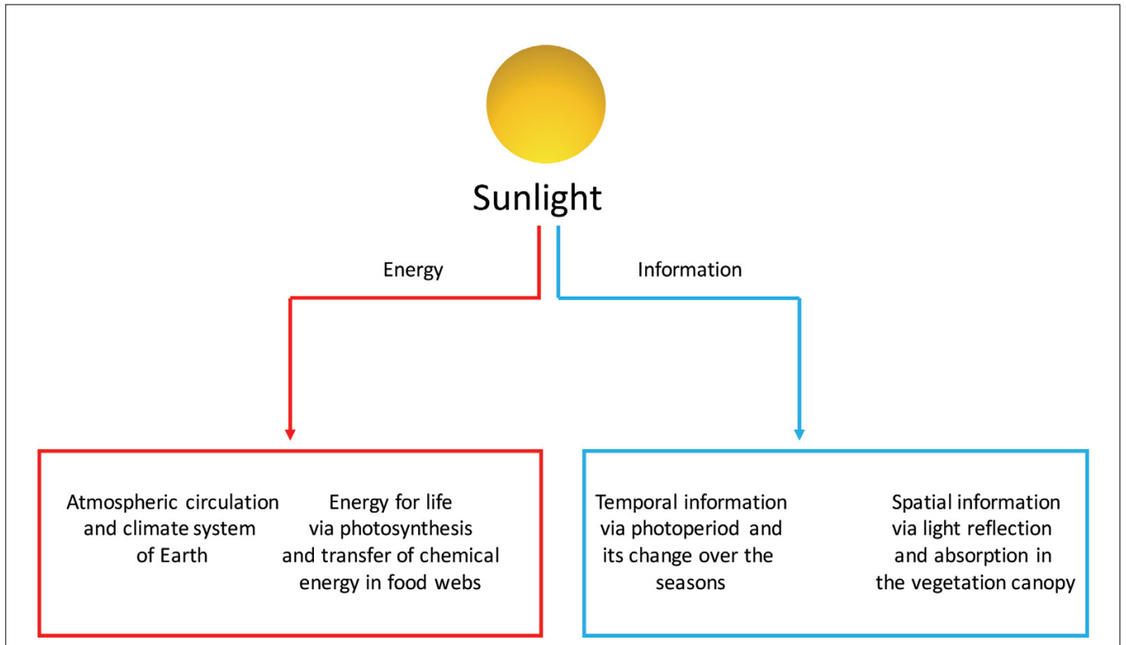

FIGURE 1. Energy and information conveyed by light. Energy from sunlight drives the Earth's atmospheric circulation and thus its climate system. It also supplies energy for almost all processes in living organisms. In addition, sunlight provides information; while this is well known on the molecular level and best explored in animals, much less is known about the information conveyed by light on the ecosystem level—especially how vegetation is affected on larger scales, up to the biome level. The photoperiod (i.e., the day–night cycle and its variation during the year) provides temporal information. Light absorption and reflection also provide spatial information and allow competitor recognition in plant canopies.

The processes regulating flux and function at the individual plant scale will not necessarily be the same as those found in the canopy or at the ecosystem scale, because not all processes relevant at one scale will be equally important at other scales (*10*). This is particularly true for plants, which are less centrally organized than animals. Research on the circadian regulation of photosynthesis and transpiration on the ecosystem scale in a field setting has received limited attention, mainly due to experimental limitations. The effect of the circadian clock is normally assessed under constant light and/or dark conditions, which is difficult if not impossible to achieve for whole ecosystems and under field settings. However, the few studies that have been published and that used either statistical filtering approaches or elaborated field infrastructure give some initial indications that circadian regulation may act as an adaptive memory to adjust ecosystem function based on environmental conditions from previous days (*11*, *12*). Still, we do not know if these clock-triggered mechanisms significantly affect the carbon and water balance of ecosystems, and if terrestrial biosphere models (which do not include these mechanisms) allow for a proper accounting of carbon sequestration and other functions of the terrestrial vegetation. Thus, global carbon and water cycles may be more complex than originally thought, if circadian memory acts not only on the molecular and individual plant level, but also on the ecosystem and biome scale. Thus, system responses may not be related only to the direct effects of environmental cues, but may also be driven by antecedent cues in the sense of an environmental memory. The diurnal and seasonal rhythmicity of daylight furnish a central source of information triggering this memory.

Circadian regulation is also responsible for part of the phenological change we observe through the seasons. Plants are often classified as either "photoperiod-sensitive" or "photoperiod-insensitive," depending upon whether

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leaf unfolding, flowering, or other life-cycle events depend on the photoperiod. Phenological events also depend on temperature and water availability, thus photoperiod is not the only important cue. As global warming advances, we are more often encountering an advancement of life-cycle events. However, such advancement has been slower than predicted based on temperature changes alone (*13*). Photoperiod signals, which do not change with warming, could thus provide a buffer against such phenological advancements.

Information conveyed by light from/about the local environment

Light provides information on the structure and quality of the environment and neighborhood within an ecosystem. This is important not only for animals and their spatial orientation, but also for sessile plants. Chlorophyll, the major light-absorbing pigment of plants, is activated predominantly by blue (400 nm–500 nm) and red (650 nm–700 nm) light, causing a depletion of these wavelengths further down in the vegetation canopy. Moreover, far-red light (700 nm–800 nm) is reflected by the leaves. This reflection also occurs downwards into the canopy, leading to an enrichment of far-red light. Thus, the ratio of red to far-red light will be reduced in dense canopies. Within complex, multilayer-canopy ecosystems such as forests and grasslands, the spatial distribution of light as well as its quality and wavelength composition allow for a 3D interpretation of available space and competitor location, and an optimization of shade-avoidance strategies (*14*). Due to the different absorption and reflectance properties of different objects, plants can differentiate between the shade of a nonliving object (e.g., a rock) and that of another plant: In the shade of a plant, far-red light is relatively enriched compared to the red light, whereas natural nonliving objects will not change the red-to-far-red ratio. Phytochrome is used by plants to measure the ratio of red to far-red light, and thus to detect whether the plant is in the shade of a competitor or not. In addition to red-light depletion, absorption of light by chlorophyll and other pigments also causes reduction of blue light in the shaded parts of dense canopies. Blue-light intensity and its change is detected through two classes of blue-light photoreceptors called "cryptochromes" and "phototropins" (*15*). These different photoreceptors regulate the concentration and allocation of various phytohormones, such as gibberellins, auxins, and brassinosteroids, which in turn affect growth patterns.

Because of their ability to sense light quality, plants can thus alter their growth strategy accordingly (so-called "photomorphogenesis"), for example by enhancing height growth to reduce competition for light. The red-to-far-red ratio also provides important information to plants about their location in the system. If sensed vertically, the red-to-far-red ratio of incoming radiation indicates how far it is to the top of the canopy (i.e., the lower the red-to-far-red ratio, the further the distance), albeit not in meters, but in terms of "competing leaf surface." By contrast, if sensed horizontally, plants can determine how far away the nearest plants are that might compete for light. Depending on

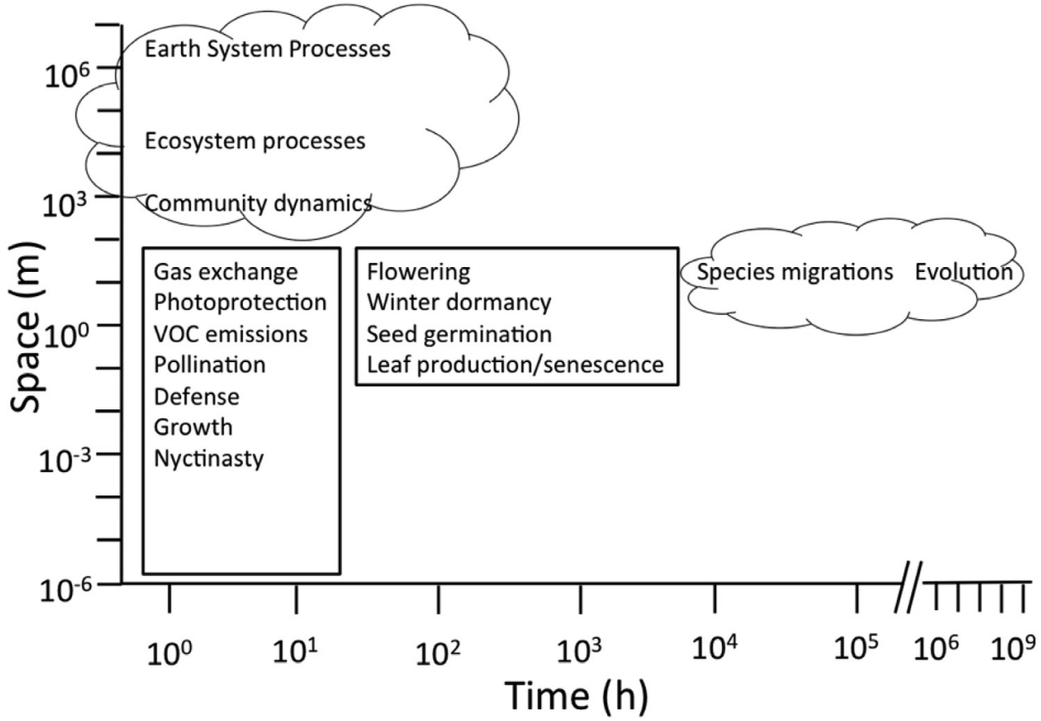

FIGURE 2. Circadian regulation of plant and ecosystem processes across scales. Circadian regulation acts on a series of processes, from organelles up to individuals, and on daily to seasonal scales (in boxes). The potential role of circadian regulation at larger temporal and spatial scales (in clouds) remains unknown. VOC, volatile organic compounds (emitted by the vegetation).

their life-history strategy, plants can adjust their growth accordingly, for example by growing away from their neighbors to avoid competition, or growing toward them so as to outcompete them.

Plants have developed different combinations of life-history traits such as growth and development rates, size and age at maturity, or lifespan in order to respond to changing environmental factors that may impact fitness. Organisms seek to maximize their fitness, which is determined by both reproductive success and survival. Because light is an important environmental factor, plant species have evolved strongly diverging morphological and ecophysiological traits to improve their fitness under differing and changing light conditions. Trees have evolved upright stems to get access to direct sunlight, with some species growing taller than others (e.g., giant sequoias in the Southwest of North America or some species of the *Dipterocarpaceae* family in Southeast Asia). Plant species such as some tall tropical forbs tend to grow extremely large leaves to collect sunlight. In contrast, the development of shade tolerance allows certain plant species to become established and survive under dense forest canopies or beneath multiple layers of herbs in grasslands. All of these traits affect the response of individual species to light, according to the information it provides on their position within the canopy and relative to their competitors.

Many open questions remain with respect to the orientation of plants within the complex canopies of forests and grasslands. For example, plants need to determine if they are shaded by parts of their own organism, such as leaves, or by competitors; and growth reactions need to be adjusted accordingly. Even though wavelength-specific reflectance and absorption patterns of different plant species may vary, conspecific competition cannot be distinguished from self-shading by sensing light quality alone. Light intensity and carbon assimilation may provide additional organism-integrating information, because the whole plant is a source-sink continuum for

assimilates. If the majority of photosynthetically active plant parts are occupying space in the canopy where a net carbon gain is achieved, heterotrophic tissues such as trunks and roots will be supplied via phloem transport with assimilates, as will leaves that are growing at lower light intensities that do not allow positive net photosynthesis. In this case, and assuming a longer-term negative carbon balance, it may be advantageous to shed these leaves. However, if most leaves fall below a critical level of carbon gain, height growth may need to be promoted to get better access to light. Thus, light-energy foraging and light-quality sensing are closely interrelated and, in combination, determine the growth strategy of plants in ecosystems.

Sunlight not only provides energy for almost all processes in the biosphere, but is also an important source of information for living organisms and ecosystems.

The spatial information provided by light undergoes temporal shifts since light quality and quantity change during the day and across the growing season. Depending on latitude and several biotic (e.g., canopy density and structure) and abiotic factors (e.g., seasonal cloudiness), the light environment in an ecosystem may be spatially more complex but temporarily (seasonally) less variable (e.g., tropical rainforest), or spatially less complex but seasonally more variable (e.g., tundra). Moreover, the light climate within a canopy also depends on phenology, which again is often triggered by the photoperiod.

Phenological cues play a key role in the persistence of the herb layer in temperate forests, (e.g., those dominated by European beech)—where most herbaceous plants need to have accomplished their seasonal cycle prior to the development of the canopy, which casts too much shade on the forest floor for other plants to survive. These herbaceous plants take day length (photoperiod) as the trigger for the beginning of their development rather than weather patterns. They would lose precious time if they lagged behind weather patterns in their development. Although this strategy is risky (since tree phenology is strongly determined by weather cues), it is the only possibility for their survival, which hinges critically upon sensing light and shows the correlation between the temporal and spatial complexity of light as a source of information and energy.

Challenges related to light information in the Anthropocene

The term "Anthropocene" encompasses all major anthropogenic changes in ecosystems, biodiversity, and biogeography, among other factors, through climate change. Human impact on light as a source of information, which is important for ecosystem processes and function, can occur via direct effects such as the increasing abundance of artificial lighting, often referred to as light pollution. Moreover, rapid environmental change induced by mankind might interfere with circadian resonance, which normally serves to tune a plant's endogenous rhythms to match environmental cues. These impacts may compromise the evolved mechanisms of plants and vegetation and disrupt their ability to predict conditions in the (near) future based on hitherto "reliable" environmental cues (e.g., day–night rhythm or seasonal rhythm).

It is not only animals, which have often adapted their behavior to the day and night rhythm, but also plants and whole ecosystems that are affected by artificial lighting. While light intensity may be only locally (close to the light source) sufficient to induce photosynthesis at night, circadian clocks and photoperiodism are likely be more strongly affected at lower light intensities via phytochrome- and cryptochrome-sensing. Changes in the natural photoperiod as a consequence of artificial lighting are known to affect plant phenology in various ways, including changing the timing of flowering as well as leaf shedding of deciduous trees in autumn. As the photoperiod's natural, reliable cue is altered, it may no longer provide an adaptive advantage to enable the plant to cope with environmental conditions, but rather turn maladaptive. As an example, delayed leaf senescence in trees close to street lamps might increase the risk of early frost damage (*16*).

Under natural conditions (i.e., in the absence of artificial light), diurnal and seasonal light-related triggers remain largely constant as climate factors are changing. Thus, the phenology of photoperiod-sensitive species may no longer be in resonance with current climatic conditions. The abovementioned buffer effect provided by temperature-insensitive photoperiod signals may therefore be diminished or may even turn negative, thus restricting the plastic response to direct environmental cues when the change in environmental conditions becomes more extreme. Our understanding of the role of light triggers in the adaptation of individual species (including adaptation by migration) and of whole ecosystems (e.g., synchronization among species, including plant–animal mutualism) is largely lacking, reducing our ability to predict impacts and devise response strategies. We do not yet know if the evolved ability of plants to predict future conditions based on aspects of the natural light regime is an advantage or a disadvantage with respect to global climate change and human-induced changes of the light regime. In general, it is assumed that prediction of conditions in the (near) future that takes advantage of "reliable" environmental cues (day–night and seasonal rhythms) optimizes resource use and provides acclimation and adaptation advantages. Circadian resonance has been repeatedly shown to be adaptive and to promote growth and survival (*17*). However, such binding to daylight rhythmicity, both on a diurnal and seasonal scale, may hamper species distribution and fast acclimation in the event of rapid environmental change. It may thus happen that the potential distribution range of a species—as defined by temperature and precipitation—moves north due to

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climate change, but that the photoperiod cues at this new latitude do not match the evolutionary demands of that species. As the climate changes faster than ever, it is unlikely that plants will have sufficient time to adapt, especially trees and shrubs with long generation times.

Conclusions

Sunlight not only provides energy for almost all processes in the biosphere, but is also an important source of information for living organisms and ecosystems. In plants, light-quality sensing and light-energy harvesting are closely interlinked and determine the growth strategies within complex canopy environments. Yet, how various sources of information are coprocessed remains unknown. The information provided by the highly reliable photoperiod allows a plant to substantially increase photosynthesis, growth, and survival when the circadian clock period and the external light–dark cycle are matched. However, whether the circadian clock plays a role in modulating canopy and ecosystem water and carbon fluxes is still unknown. If ecosystem responses are also driven by antecedent environmental conditions via the circadian clock, Earth system models may be unable to fully capture the effect of global climate change on the Earth's biogeochemical cycles. Taking light and photoperiod as surrogates for other, less reliable environmental cues, such as temperature and precipitation, may prove to be an insurmountable evolutionary burden for some species, particularly when light and other environmental cues no longer match, preventing migration, for example. Neither species distribution models nor mechanistic dynamic global vegetation models normally take into account the impacts of natural light as a source of information. Thus, we need better mechanistic representations of the impacts of light information on ecosystem processes in order to include these in models that allow for the projection of future species distributions as well as ecosystem and biome function.

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